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ON THE AFFINITIES OF TARSIUS: A CONTRIBUTION TO THE PHYLOGENY OF THE PRIMATES.

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In order to form a just estimate of the zoological rank of an animal in the system we must take into consideration its whole organization and development. Any system of classification which only considers one set of organs at the exclusion of the others will probably lead to false ideas as to the systematic position of the animal in question. In endeavoring to determine the relationship of *Tarsius* to the other members of the Primates, we are met at the outset with that great difficulty in morphological enquiry to decide between characters due to inheritance and those arising from convergence. The phenomenon of homoplasy is being recognized more and more by naturalists, and it is only by a complete knowledge of the palæogenetic history of a phylum that we can decide surely whether certain characters of the skeleton, common to it and to other phyla, are homogenetic or homoplastic in their origin.

Tarsius stands preëminently among Mammals as one of the most interesting of generalized types, for in this genus we have an animal whose assemblage of characters relates it on one hand to the Apes, and on the other surely to the Lemurs. The question arises, is the position tenable if I maintain that as *Tarsius* exhibits many fundamental structural peculiarities only found in the Apes and Lemurs, as a result the Anthropoids and Lemuroids may be considered genetically related. I may add that the palæontological evidence supports this conclusion.

I find on further study that Mivart's views concerning the relations of the Lemurs and Apes are most unsatisfactory. He considers that the question of genetic relationship in classification should take a subordinate place, and if two groups of animals exhibit characters in common, it makes little difference whether the characters be due to convergence or were inherited from a common ancestor which gave origin to the two aggregations in question. In short, to Mivart classification is merely a convenience, and may or may not denote genetic relationship. Applying these principles to the arrangement of the Primates, Mivart merely placed the Lemurs and Apes together because they exhibit some characters in common, and not that he considered these two suborders of the Primates closely related. Since Mivart's important paper on "Lepilemur and Cheirogaleus" was written in 1873, great strides have been made in arranging some of the Mammals based on the true scientific principle of community of descent. A good example of the determination of adaptive versus essential characters is the case of the Carnivora, where the important discoveries of vertebrate palæontology clearly demonstrate that the Bears and Dogs are related, but the Mustelines, instead of being connected with the Bears, are related to the Civets. Again, the Hyenas came off the same stem as the Mustelines, and are related also to the Viverrines and not to the Cats, as supposed by Flower.

Burmeister, the monographer of *Tarsius*, considered this animal to be a Lemur, but with characters relating it to the Apes and also to the Insectivora. Burmeister's views as to the relationship of *Tarsius* is shown in the following passage from his Memoir: "Aber *Tarsius* ist nicht mal ein Affe, er ist vielmehr nur ein Halbaffe, ein Mitglied jener Gruppe, innerhalb welcher die frugivore oder zugleich omnivore Nahrung der hochsten Säugethiere in die ausschliesslich animalische zunächst insektivore, uberspringt." That Burmeister fully appreciated the essentially lemurine characters of *Tarsius*, and which I should like to emphasize, do not occur in any other Mammalian group except in the Lemurs, is evident from his paper. Hubrecht, who has recently written an important paper on the placentation of *Tarsius* insists on the close relationship between this genus and the Apes. Because Hubrecht finds that the histological structure of the placenta and the stalk connecting it with the embryo in *Tarsius* is structurally like that of the Anthropoids, he proposes to overthrow our present system of classification of the Primates, dividing this group into two distinct orders, and placing *Tarsius*, also the fossil genus *Anaptomorphus*, among the Apes. I believe that Hubrecht, in his discussion of the systematic position of *Tarsius*, has not taken into consideration the whole organization of this genus, and furthermore I am of the opinion that any classification of the Mammalia depending solely on the structure of the placenta and its connections will prove to be unreliable.

I am aware that there are many difficulties in the way of claiming that Lemurs and Apes are genetically related, but if one eliminates some of the highly adaptive and specialized characters of the Lemurs, which appeared late in their evolution, then these two groups of Mammals approach each other very closely and on osteological characters alone, we are unable at present to surely separate the early Lemurs from the Apes. In other words, the extinct Lemurs possess certain characters which are now found widely separate in the two suborders of recent Primates.

In order to allow the reader to form an unbiased opinion of the affinities of *Tarsius*, I will briefly review Hubrecht's important contribution to the placentation of *Tarsius*, and follow him in his comparison of the placental connections of *Tarsius* with that of *Erinaceus*, a typical Insectivore, and also compare both with what is known of the placentation in the true Lemurs.

In the early as in the later stages of *Tarsius*, the yolk sac only takes up a small portion of the cavity of the blastocyst, and there is never present an omphaloide placentation as in *Erinaceus*. In this character of its development *Tarsius* strictly follows the plan of the Anthropoids.

A very important point in the early development of *Tarsius* is that the surface of the chorion never becomes entirely villous as in man. In *Cercocebus* the villosities of the chorion are limited to dorsal and ventral areas. The fact that *Tarsius* has omitted this diffuse stage of the placenta found in the true Anthropoids, clearly shows that this is a specialization in the development of this genus. Hubrecht remarks in referring to this completely villous stage of the chorion of the Anthropoids: "Ich halte den Zustand welcher beim Menschen und Anthropoiden sich erhalten hat, fur sehr primitive." Again, he says: "Somit neige Ich zu der Ansicht hin, dass in diesem ununterbrochenen Zottenpelz ein primitiver charakter erhalten, und dass die partielle Zottenbildung von Niederen Affen, wie der Fig. K giebt; eher als ein abgeleiterer Zustand zu betrachten sei."[1] The reference he gives to Fig. K is the condition found in *Cercocebus*, where the villous areas of the chorion are restricted to patches above and below the fœtus. In *Erinaceus* the amniotic cavity is formed by a splitting of the epiblast, so that the portion of this membrane below the amnion is the only part directly concerned in the growth of the embryo; accordingly Hubrecht designates this as the epiblast proper, whereas the remainder of the epiblast not used in the formation of the embryo he calls the trophoblast. Prof. Hubrecht considers the development of the amnion as occuring in *Erinaceus* the primitive one, whereas the more ordinary way by folds growing over the embryo and uniting, as a secondary process. *Tarsius* follows the more normal formation of the amnion by the folding off of the embryo.

In an early stage in the development of *Tarsius*, there occurs a thickening in the external epiblast or trophoblast, and on the opposite side from the embryonic area, this is the placental "anlage" or rudiment. It is important to notice that the first indication of the placenta is situated ventrally in relation to the embryo, as in the Apes it is dorsal. Again, the origin of the placenta in *Tarsius* has no connection whatever with the allantois, and the latter organ never becomes directly connected with the placenta as will be shown later. At the time of the origin of the placental " anlage " in *Tarsius* the whole blastocyst is lined by the mesoblast and in the portion of the latter which connects the placental anlage with the posterior end of the embryo, originates a very important structure, highly characteristic of the Anthropoids; this is the bauchstiel or ventral stalk. Prof. Hubrecht explains the genesis of the bauchstiel very clearly, and shows that as the embryo becomes folded off from the yolk by the development of the amnion, that this mesoblastic strip is carried with the embryo until the latter is really suspended in the cavity of the blastocyst, its only attachment to the wall of the same is by means of the bauch- or haftstiel as he calls it. Vascularization of the ventral stalk soon takes place by blood-vessels arising in it, and thus embryo and placenta are brought into vascular connection. Another very important point shown by Hubrecht is that the portion of the bauchsteil next to the embryo is permeated by two tubes, the dorsal is a prolongation of the amnion and the lower is the rudiment of the allantois. The latter is one of the most important discoveries made by Hubrecht in connection with the development of *Tarsius*, as he demonstrates that in *Tarsius*, as in the Apes and Man, the allantois is rudimentary and does not hang freely in the coelomic cavity as in the rest of the Mammalia. Prof. Hubrecht shows that the allantois rudiment takes no share in the vascularization of the bauchstiel as the following quotation proves: " Finden wir in dem Haftstiel eine verhältnissmässig langen Restbestand dieses Allantois rohres, welches aber, wie bereits auseinander gesetzt wurde, an der Vaskularisation des Haftstiels keinerlei antheil hat." Professor Hubrecht compares an early stage of *Erinaceus*, before the splitting of the mesoblast (see his paper, stage 2), with that of *Tarsius* (fig. 7), in order to prove that *Erinaceus* has a sort of bauchstiel, connecting the rear end of the embryo with the trophoblast. In this stage of *Erinaceus* the extent of the mesoblast is very limited, but in *Tarsius* the whole blastodermic vesicle is lined by mesoblast.

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[1] Die Keimblase von Tarsius, Leipzig, 1896, pp. 171 and 172.

Turning now to the fœtal membranes of the Lemurs, we find there is apparently little in common between the placentation of these animals and *Tarsius*. In *Tarsius* the placenta is diskoidal-deciduate, whereas in the Lemurs it is diffuse and nearly the whole surface of the chorion is villous. It appears then that we are dealing with two types of placentation fundamentally different in structure and origin; however, the early development of the placenta in the Lemurs is totally unknown so far as I have been able to learn. Turner has described the placentation in the genus *Lemur*, and Alphonse Milne-Edwards in the Indrisine Lemurs. In all known forms of Lemurs the allantois is a huge sac enveloping the embryos, and often having numerous diverticulæ. Milne-Edwards calls attention particularly to one point, that the external layer of the allantois has no intimate connection with the chorion, and moreover it is not vascular. The question then arises, if the allantois takes no share in the formation of the placenta in the Lemurs, the latter organ probably originates from the chorion as in the Apes. This point is not yet proven, and it remains for further research to find out how the connection between fœtus and chorion is brought about in the Lemurs.

Dr. Charles Sedgwick Minot, to whom I am greatly indebted for an important letter on the question of the placentation of the Primates, in his great work on "Human Embryology," divides the placentation of the Mammalia into two types, in the first group the allantois is large and supplies the chorion with its blood-vessels; this is the condition occurring in the majority of the Mammalia, excepting some of the Primates. In the more highly differentiated Anthropoidea, the allantois takes no part in the formation of the placenta, and the blood-vessels arise in the chorion and bauchstiel *in situ.* Dr. Minot designates this type as chorionic placentation. I quote two passages from his letter which have an important bearing on the question of the relations of the placentation of the Apes to that of the Lemurs: "Unfortunately, nothing satisfactory is known of the early stages of Lemurs, which are the critical ones for placental homologies, but as far as our fragmentary knowledge goes, I fail to recognize any impossibility of regarding the placentas of Monkeys and of Lemurs as of one fundamental type." Again Dr. Minot says: "Whether a placenta is diffuse or not cannot decide as to its homologies, for the human placenta is diffuse to start with, yet has nothing in common with the Ungulates, *though it may be compared, apparently, directly with that of the Lemurs.*"

I am not, at present, in a position to discuss the whole organization of the Lemurs, and will merely refer to the brain and female reproductive organs. In regard to the structure of the brain in the Lemuroidea, it may be said that the genus *Lemur* has a lower type of encephalon than is found in the *Indrisinæ.* As compared with the *Insectivora,* the brain of the Lemurs is in a much higher stage of development, and approaches nearer that of the *Cebidæ* than any other group. In *Lemur* the frontal lobes of the cerebrum are narrow, and the olfactory lobes are plainly visible in front; however, in *Propithecus,* the frontal portion of the cerebrum is quite highly developed, being as broad as in the American Monkeys, and contains secondary convolutions not seen in the lower forms of Lemurs. Again it is to be noted that in the Lemurs as in the Apes, the sylvian fissure is largely developed and extends a good ways superiorly on the hemispheres, and this character is particularly noticeable in the *Indrisinæ.* The antero-temporal sulcus is also well-marked in the Lemur's brain, and resembles this fissure in the Anthropoids. The posterior lobes of the cerebrum remain in a primitive condition, and the cerebullum is exposed as in the lower Mammalia. Prof. Flower calls particular attention to the presence in the brain of the Lemurs of the calcarine fissure which is so characteristic of the higher Primates, and speaking in general of the sulci of the inner part of the cerebrum of the Lemur's brain, Prof. Flower remarks that they follow also those of the Anthropoidea. The general configuration of the frontal lobes in *Nyctipithecus* among American monkeys is like that of *Propithecus,* but in the former the surface of the hemispheres is smoother and lacks the smaller convolutions seen in the *Indrisinæ.* Again, in *Nyctipithecus* the olfactory lobes project considerably beyond the cerebrum. In conclusion it follows from the above that the brain of the Lemurs is much more primitive than that of the Apes, but may represent a stage in the evolution of the brain which leads to the higher differentiated encephalon of the Anthropoids.

(*To be continued.*)